Vol. 113. Pt. 12. Pp. 369–386. 10 figs. 8th December 1961

COMMONWEALTH INST. OF ENTOMOLOGY LIBRARY
11 DEC 1961
Eu.344
SERIAL SEPARATE

THE TRANSACTIONS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

PAGE

TAYLOR, L. R. and CARTER, C. I. The analysis of numbers and distribution in an aerial population of MACROLEPIDOPTERA 369-386
10 figs.

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 8s. 0d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded 1833. Incorporated by Royal Charter 1885

Patron:
HER MAJESTY THE QUEEN

OFFICERS AND COUNCIL FOR THE SESSION, 1961–1962

PROFESSOR G. C. VARLEY, *President*
MR. R. B. BENSON, DR. N. E. HICKIN, MR. M. J. WAY } *Vice-Presidents*
DR. C. G. BUTLER, *Treasurer*
DR. PAUL FREEMAN, *Secretary*
MR. W. H. POTTS, *Editor*

Other Members of Council

PROFESSOR D. S. BERTRAM
DR. M. I. CRICHTON
DR. K. U. CLARKE
MR. R. G. DAVIES
DR. A. M. EASTON
DR. J. E. HARKER
DR. P. T. HASKELL
DR. B. R. LAURENCE
MR. H. OLDROYD
SIR BORIS UVAROV, K.C.M.G., F.R.S.

MISS E. EVANS, *Registrar*

Finance and House Committee

PROFESSOR D. S. BERTRAM (*Chairman*)

MR. J. P. DONCASTER
DR. J. A. FREEMAN, O.B.E.
DR. N. E. HICKIN
DR. D. J. LEWIS
MR. M. E. SOLOMON

Publication and Library Committee

MR. R. G. DAVIES (*Chairman*)

DR. J. D. CARTHY
DR. P. T. HASKELL
DR. C. G. JOHNSON
MR. D. LEATHERDALE
MR. G. E. J. NIXON

Conservation (Insect Preservation) Committee

MR. R. B. BENSON (*Chairman*)

DR. B. M. HOBBY
MR. T. G. HOWARTH
DR. A. M. MASSEE
MR. F. T. VALLINS
MR. M. J. WAY

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   Dr. H. E. Hinton, F.R.S., appointed 1958.
2. **Local Committee of Management of Wicken Fen.**
   Dr. John Smart, appointed 1960.
3. **National Trust for Places of Historic Interest or Natural Beauty.**
   Mr. N. D. Riley, C.B.E., appointed 1955.
4. **New Forest Association.**
   Mr. C. W. Mackworth-Praed, appointed 1948.
5. **New Forest Joint Committee.**
   Lt.-Col. F. C. Fraser, appointed 1949.
6. **Field Studies Council.**
   Dr. W. H. Thorpe, F.R.S., appointed 1944.
7. **Yorkshire Naturalists' Trust, Ltd.**
8. **The Biological Council.**
   Dr. N. E. Hickin, appointed 1952.
9. **The Parliamentary and Scientific Committee.**
   Dr. N. E. Hickin, appointed 1953.
10. **British Co-ordinating Committee for Nature Conservation.**
    Mr. R. B. Benson, appointed 1960.
11. **Council for Nature.**
    Dr. N. E. Hickin, appointed 1958.

THE ANALYSIS OF NUMBERS AND DISTRIBUTION IN AN AERIAL POPULATION OF MACROLEPIDOPTERA

By L. R. Taylor and C. I. Carter

(*Rothamsted Experimental Station, Harpenden, Herts.*)

Manuscript received 24th January, 1961

(Read 3rd May, 1961)

With 10 Text-figures

Contents

		PAGE
I.	Introduction	369
II.	The site, traps and trapping procedure	370
III.	Suction trap analysis	371
	(1) Numbers in flight	371
	(*a*) Population structure	372
	(*b*) Moths and butterflies	373
	(*c*) Phenology	373
	(*d*) Weather and flight	373
	(2) Distribution in time and space	373
	(*a*) Diurnal periodicity	373
	(i) *Amphipyra tragopoginis*	374
	(ii) *Agrochola lychnidis*	374
	(iii) Other moths	374
	(*b*) Height of flight	375
	(i) *Amphipyra tragopoginis*	375
	(ii) *Agrochola lychnidis*	375
	(iii) Other moths	376
IV.	Comparison of light and suction traps	378
	(1) The effect of light on the apparent commonness of moths	378
	(2) The effect of light on the apparent distribution of moths	382
	(*a*) Time of flight	382
	(*b*) Height of flight	383
V.	Acknowledgments	385
VI.	Summary	385
VII.	References	385

I. Introduction

The Macrolepidoptera of England are the most thoroughly trapped and recorded group of insects in the world. Nevertheless, there are remarkably few published records of unbiased samples of the flying adult populations of these insects, perhaps because most samples have been collected by light or bait traps, which do not sample randomly; the number of any species caught depends, not only on their commonness, but also on the attractiveness they find in light or scent. Quantitative data from these traps is therefore suspect.

Suction traps do not depend for their sampling power upon physiological responses of the insects and hence are free from the major element of bias; no trap gives a completely random sample, for its mere presence must have some effect on the environment. We now have hourly catches of Macrolepidoptera from a vertical

series of suction traps for several months in three successive years, so that it is possible to reconsider some aspects of flight behaviour, such as height of flight and periodicity, temperature relations and population structure in successive years. Insects so relatively rare as moths and butterflies are caught only in small numbers, *i.e.* 0·6 specimens per trap per day. It is therefore of particular interest to see how much information can be obtained from such small, but reliable, samples, and it is also possible to investigate some of the effects of the attractiveness of light in light trap catches.

II. The Site, Traps and Trapping Procedure

Four 12-inch suction traps were hung from a tower, one at 9 feet, one at 21 feet and two at 56 feet; in addition there was a 30-inch trap at 500 feet (1953) or at 250 and at 1000 feet (1954–55) (Johnson and Taylor, 1955*a*, *b*). No Macrolepidoptera were caught above 56 feet. The site, at Cardington, Bedfordshire, England, has been described in detail elsewhere (Giblett *et al.*, 1932; Johnson, 1957). The traps were in a large expanse of poor pasture with an arable field about 50 yards to the south. About 50 yards to the north was a small stream. Meteorological records were kept at the site. The temperatures were taken by 24-hour thermograph in a 5-foot Stevenson screen, *i.e.* routine Meteorological Office records.

In 1959 a light trap was used; it was of standard Rothamsted pattern (Williams, 1948) with a 200 watt combined M.V. and tungsten filament bulb (Siemens MBT/U). It was at a height of 2 feet 6 inches, 100 yards from the suction trap site.

Suction traps worked most days between 24th September and 21st October, 1953; 25th July and 28th October, 1954; 21st July and 18th October, 1955. The light trap worked each night from 24th August to 14th September, 1959. Greenwich Mean Time is used throughout.

For nomenclature Kloet and Hincks (1945) have been followed. Estimates of density are given as mean number of insects caught per 1,000,000 cu. ft. air. For example, *Agrochola lychnidis* was found to fly only between 15·00 hours and 03·00 hours, a maximum of 12 hours per night. If only one insect was caught by all four traps, each collecting 83,100 cu. ft. of air/hr., in one night, then the mean density is considered to be 1 per $4 \times 12 \times 83100 \times 0{\cdot}5$ cu. ft. of air, *i.e.* $D_e = 0{\cdot}5$ per 10^6 cu. ft. of air. The factor 0·5 corrects, provisionally, for the measured efficiency of 12 inch suction traps in extracting insects from the air collected in these conditions, *i.e.* 50 per cent. (Taylor, *in preparation*). When densities are given in this way the figures are all strictly comparable both within and between species; the traps are standardised to work at all times and in all kinds of weather (Taylor, 1955, and *in preparation*). Such estimates of the absolute density are of little importance in illustrating, for example, diurnal periodicity; in these instances the scale given in the ordinates has not been converted and is merely an index of density for one part of the figure relative to another.

Table I.—*Highest recorded mean density (per 10^6 cu. ft. of air) during single hours, for single species*

Height (feet)	Date	Time (G.M.T.)	Species	Catch	Density
21	6.ix.1953	17.00–18.00	*Ag. lychnidis*	21	504
21	7.ix.1955	16.00–17.00	,, ,,	10	240
21	12.ix.1955	16.00–17.00	,, ,,	10	240
21	26.viii.1954	20.00–21.00	*Amph. tragopoginis*	9	216
9	31.viii.1954	19.00–20.00	,, ,,	8	192

III. Suction Trap Analysis

(1) *Numbers in flight*

The noctuids, *Amphipyra tragopoginis* (the Mouse) and *Agrochola lychnidis* (the Beaded Chestnut), were the only two species sufficiently common to analyse individually in detail; only these two species had catches exceeding two in one trap in any one hour. Both species were present in 1954 and 1955. In 1953, trapping was started too late in the season for most species and only *Ag. lychnidis* is considered. The largest catches in any single hour are given in Table I.

The highest catch on a single night was 40 (26th–27th August, 1954) of which 36 were *Amph. tragopoginis*. The highest density of 504 *Ag. lychnidis* per 10^6 cu. ft. of air may be compared with the maximum recorded density for *Aphis fabae* Scop. over a highly infested bean crop, *i.e.* 165,000 per 10^6 cu. ft. of air (Johnson, 1952). The volumes of these two insects are in the ratio of about 215/1; the airborne biomass of the moth is therefore almost equal to that of the aphid. This is a very high density.

Table II.—*Species list of Macrolepidoptera from Cardington, Beds., suction traps 1953–4–5*

	1953	1954	1955	1954+55
Amphipyra tragopoginis (L.)	.	225	269	.
Agrochola lychnidis (Schiff.)	58	23	88	.
Triphaena pronuba (L.)	.	13	8	.
Xylophasia monoglypha (Hufn.)	.	11	7	.
Amathes c-nigrum (L.)	.	5	5	.
Apatele rumicis (L.)	.	5	4	.
Mamestra brassicae (L.)	.	2	1	.
Leucania impura (Hb.)	.	1	1	.
Aporophyla lutulenta (Schiff.)	.	5	0	.
Triphaena comes (Hb.)	.	4	0	.
Xylophasia lithoxylea (Schiff.)	.	4	0	.
Euxoa tritici (L.)	.	3	0	.
Phlogophora meticulosa (L.)	.	2	0	.
Apatele psi (L.)	.	2	0	.
Celaena secalis (L.)	.	1	0	.
Cosmia trapezina (L.)	.	1	0	.
Ellopia prosapiaria (L.)	.	1	0	.
Luperina testacea (Schiff.)	.	1	0	.
Phragmatobia fuliginosa (L.)	.	1	0	.
Procus fasciunculus (Haw.)	.	1	0	.
Sterrha emarginata (L.)	.	1	0	.
Euxoa nigricans (L.)	.	.	30	.
Agrotis ypsilon (Rott.)	.	0	2	.
Apatele megacephala (Schiff.)	.	0	2	.
Leucania pallens (L.)	.	0	2	.
Melanchra persicariae (L.)	.	0	2	.
Anchoscelis litura (L.)	.	0	1	.
Diarsia rubi (Vieweg)	.	0	1	.
Diataraxia oleracea (L.)	.	0	1	.
Epirrhoë alternata (Muell)	.	0	1	.
Episema caeruleocephala (L.)	.	0	1	.
Scoliopteryx libatrix (L.)	.	0	1	.
Xanthorhoë spadicearia (Schiff.)	.	0	1	.
Nymphalis io (L.)	.	1	0	.
Pieris rapae (L.)	.	0	1	.
Polyommatus icarus (Rott.)	.	0	1	.
Number caught (N)	58	313	430	743
Number of species (S)	.	22	22	36
Index of diversity, α (per cent.)	.	5·1±13	4·9±12	7·8±9

(*a*) *Population structure*

Table II is a list of species, with the numbers caught each year arranged in order of commonness. Eight species occurred in both years and in the same order, suggesting a constant resident population ; but those species that occurred only in one year may not be residents. These species have one to five specimens each, except *Euxoa nigricans*, which was probably missed in 1954 because of trap failures. Of the 28 species caught in only one year, 14 were caught in 1954 and 14 in 1955, so that quantitatively the population structure (excluding *E. nigricans*) appears similar

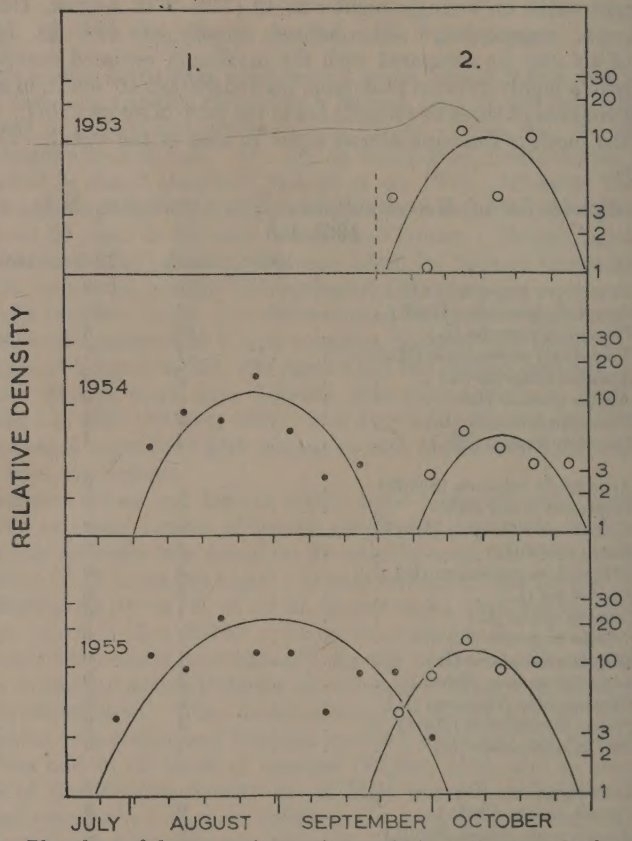

Fig. 1.—Phenology of the two major species caught in suction traps in three years (based on log. density). (1) *Amphipyra tragopoginis ;* (2) *Agrochola lychnidis.*

in the two years. The rarer species differ qualitatively in the two years and the difference can be assessed by Williams' (1947) Index of Diversity (α), that measures the relationship between numbers and species independently of the sample size. Thus the population structure of each year can be compared with the population for the two years taken together. As expected from the lists, α and its estimated standard deviation are almost identical for the two separate years (5·1 $\pm$ 13 per cent. ; 4·9 $\pm$ 12 per cent.), but when the two samples were taken together, the proportion of species with one individual is greater than expected ($\alpha = 7{\cdot}8 \pm 9$ per cent.). This suggests that some of these species (about 10) are not of the resident population but are casual visitors. Even with such a small sample, a useful estimate of migration, or the fluidity of a population, can be made provided that the sample is quantitatively reliable.

(*b*) *Moths and butterflies*

With suction traps the numbers of day-flying and night-flying insects can be compared. Of 791 Macrolepidoptera, only three individuals were butterflies. Visual impressions were that the site was poor in butterflies; the commonest species, *Coenonympha pamphilus L.*, was not caught because of its characteristically low flight among the grass, *i.e.* at about 6 inches to 2 feet 6 inches from the ground. *Nymphalis io* (the Peacock), one of the most powerful flyers of the local butterflies, was represented by a single specimen, as was *Pieris rapae* (the Small White), a medium-sized butterfly, and *Polyommatus icarus* (the Common Blue), a small weak butterfly, which shows that the trap did not select small insects unduly.

(*c*) *Phenology*

Seasonal periodicity of insect flight is very easily measured by any kind of trap. It is interesting to see how small a catch is adequate for this. Figure 1 shows the seasonal periodicity of the two common species, based on the log. aerial density. The population rise and fall is adequately depicted by even the small catches of *Ag. lychnidis*; the larger catches of *Amph. tragopoginis* do not add appreciably to the information.

(*d*) *Weather and flight*

The major weather factor is undoubtedly temperature, and the temperature thresholds are clearly demonstrated. Hourly catches were plotted against the maximum temperature during the hour. The resulting scatter diagrams (fig. 2) show almost no flight below about 8° C. for either *Amph. tragopoginis* or *Ag. lychnidis*.

The catch above the flight threshold of aphids is limited only by the size of the local field population, which can fluctuate so violently that no steady maximum is reached (Taylor, 1957). With the moths, however, the available population is fairly constant for a long time and there is a maximum to the possible sums of numbers caught in flight in a given interval of time or temperature. Figure 3*A* shows the integral curves of numbers in flight at 1° C. temperature intervals and in figure 3*B* the differential curves show the frequency distribution of the temperature threshold in these particular populations of these two moths.

These thresholds are close together and very low for an all or none function such as flight: *Amph. tragopoginis* at 10·5° C. and *Ag. lychnidis* at 9·0° C. Temperature is falling during the flight of these moths and this means that the thresholds are for continued flight as distinct from take-off; the take-off threshold may be higher. The great difference in spread of the threshold between the populations of the two species (*see* fig. 3*B*) may be caused by a greater variability between individuals of *Amph. tragopoginis* than *Ag. lychnidis*, but the rate of change of temperature associated with the response and previous temperatures may also affect this. The smaller numbers found at higher temperatures are associated with higher light intensity and this is part of the problem of diurnal periodicity, which will be dealt with under that heading. Rainfall, wind and humidity may affect flight to some extent but analysis is not attempted with this limited material.

(2) *Distribution in time and space*

(*a*) *Diurnal periodicity*

The two species that were common enough to give a complete picture of diurnal periodicity both showed an initial peak of numbers in flight followed by a "tail" of lower numbers, a gradual shift in time of flight with the change in time of sunset, and periodicity consistent from year to year. Hourly catches have been summed over several weeks to give smooth periodicity curves:

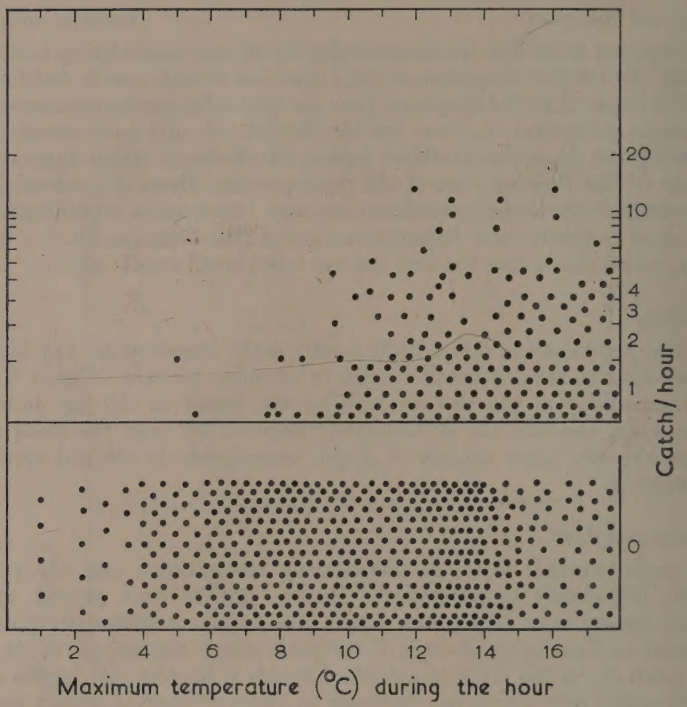

FIG. 2A.—Scatter diagram of catch × temperature: *Amphipyra tragopoginis;* 1954 and 1955 grouped. (Each point represents a single hour's catch plotted against the maximum air temperature during that hour. The ordinate scale is logarithmic and hence the zero catches are plotted separately in the lower part of the figure. Catches are plotted in the ordinate intervals to avoid overlapping points, *e.g.* any point in the ordinate interval between 1 and 2 represents a catch of one insect; in the interval 2 to 3 represents a catch of 2, *etc.*)

(i) *Amphipyra tragopoginis.*—This species flew for about ten weeks and the shift in time of flight with sun time is evident when the first five weeks are compared with the second (fig. 4*A*, *B*). Flight begins with a large peak commencing just after sunset and ending at midnight, followed by a fairly uniform lower level of flight until dawn.

(ii) *Agrochola lychnidis.*—Flight occurs only for about one month, so that sunset does not vary enough to produce a measurable change in flight time. But flight is obviously closely connected with light and the periodicity is consistent from year to year (fig. 5*A*, *B*, *C*). Flight starts as much as two hours before sunset, reaches a peak just after sunset and falls again within about two to three hours. This peak is followed, as in *Amph. tragopoginis*, by a tail of small numbers until between midnight and dawn.

(iii) *Other moths.*—Enough of five other moths were caught to show the periodicity of the species separately. Four of these (*Xylophasia monoglypha* (Dark Arches), *Triphaena pronuba* (Large Yellow Underwing), *Amathes c-nigrum* (Setaceous Hebrew Character) ,*E. nigricans* (Garden Dart)) appear in figure 10, where they are compared with light trap catches; the fifth species, *Apatele rumicus* (Knot Grass), appears in figure 6, *C*. The remaining species, with fewer individuals, *i.e.* from one to five per species, are combined; both the curve from species with one individual (fig. 6*A*) and that for species with two to five individuals (fig. 6*B*), appear to be bimodal, yet

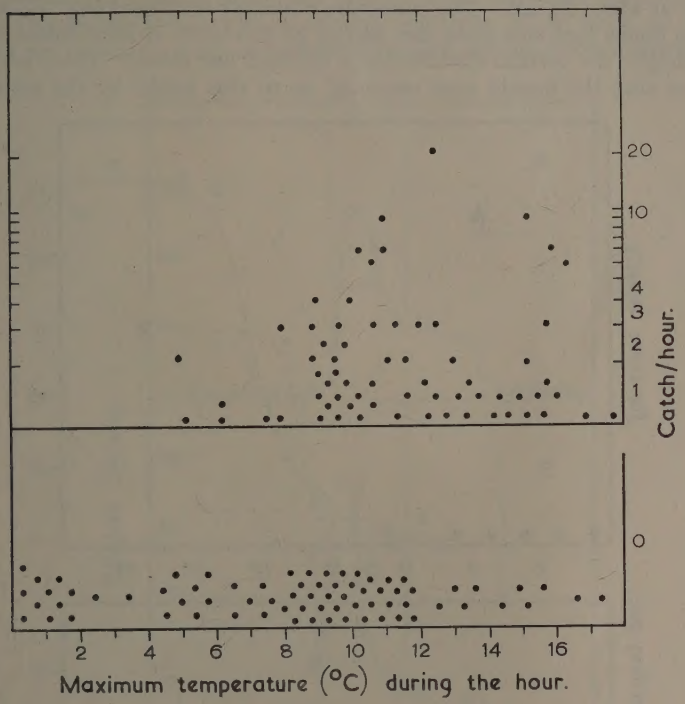

FIG. 2B.—Scatter diagram of catch × temperature : *Agrochola lychnidis* ; 1954 and 1955 grouped.

the individual species in these grouped catches show no bimodality. Of the species dealt with individually, only *X. monoglypha* (fig. 10*A*) could be said, with any confidence, to show bimodal periodicity. The most typical form of flight periodicity curve found is a peak followed by a tail (*Amph. tragopoginis*, *Ag. lychnidis*, *T. pronuba*, *E. nigricans*, *Am. c-nigrum*, *Ap. rumicus*). The bimodal periodicity sometimes demonstrated for Noctuidae by bait traps (*e.g.* Larsen, 1943) may be caused partly by combining species with different single peaks of flight, as in figure 6*A* and *B*.

(*b*) *Height of flight*

Information about the height at which insects fly is usually obtained from subjective observation. The use of traps both at high (Johnson, 1957) and at low levels (Taylor, 1960) shows that the mean density continuously diminishes as height increases; this can largely be explained by the dispersive processes of daytime air movement. The insects studied have all been small day-flying species ; these results are not expected to hold for night-flying, or for large insects with powerful flight.

Only two moths were common enough for separate analysis in more than one year, and figure 7 shows their mean yearly density × height profiles and the profile for the remaining species combined.

(i) *Amphipyra tragopoginis*.—In 1954 and 1955 the density diminished continuously with increase in height (fig. 7*A*), at least above 9 feet ; if there is a maximum density it is below 9 feet. On two occasions the catch for one night was large enough to examine separately ; on one of these nights there was a decrease in density below 20 feet (fig. 7*B*). This will be discussed later.

(ii) *Agrochola lychnidis*.—For three consecutive years the maximum density each

night was at about 20 feet. The curves are strikingly consistent (fig. 7*C*), and there can be no doubt that this moth flies mainly at this level, at least before midnight. After midnight the vertical distribution is different (*see below*). There is no reason to suppose that the insects were attracted up to this height by the trap, for the

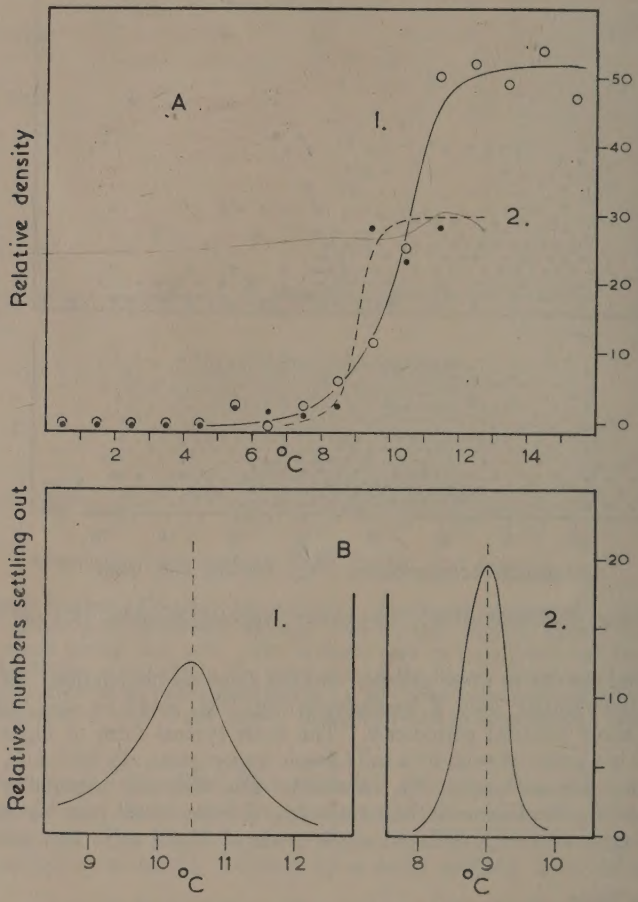

Fig. 3.—(*A*) Integral curves of numbers in flight, 1954 and 1955 summed in 1° C. intervals of temperature: (1) *Amphipyra tragopoginis*; (2) *Agrochola lychnidis*. (*B*) Differential curves, from 3 (*A*), showing flight thresholds: (1) *Amphipyra tragopoginis*; (2) *Agrochola lychnidis*. – – – – – = mode.

traps at each height were the same and there is no tree canopy. The phenomenon was not associated with temperature inversions, unlike the migratory flights of *Loxostege sticticalis* L. which, according to Melnichenko (1936), remain within the warmer air of inversions and rise with them from 23–26 feet in the evening to 250–330 feet by the morning. We offer no explanation for this curious behaviour, but it strikingly confirms that whereas small day-flying insects owe their distribution to dispersal processes of the air, large or night-flying insects may choose their own height of flight. The maximum speed of flight of *Ag. lychnidis* is 10 m.p.h., measured in the laboratory, and so it has full control of flight on most occasions.

(iii) *Other moths.*—Catches for all other species of moths show a continuously diminishing density as height increases, both for 1954 and 1955 (fig. 7*D*). No Macrolepi-

doptera were caught above 56 feet; this does not mean that they never occur there, only that the density is below the maximum sensitivity of the traps, *i.e.* less than 2·5 insects per 10^6 cu. ft. of air, so that the chance of capture is extremely low.

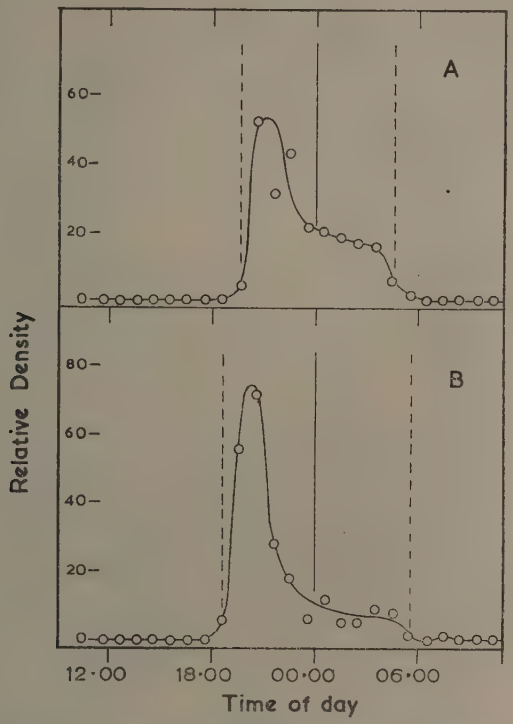

Fig. 4.—Flight periodicity of *Amphipyra tragopoginis* showing the shift in flight time with time of sunrise and sunset (– – – – –), 1954 and 1955, summed in hours: (*A*) 1st 5 weeks flight; (*B*) 2nd 5 weeks flight.

By summing catches for all years, height distribution profiles were obtained for seven separate species. In addition, profiles were obtained for the remaining insects in two batches, all species represented by only one insect and those species with two to five individuals. These nine profiles fall into three groups (fig. 8); *Ap. rumicis* and the batch with one individual per species have continuously diminishing densities, like *Amph. tragopoginis* (fig. 8*A*); *E. nigricans* and *X. monoglypha* have a prominent maximum at about 20 feet, like *Ag. lychnidis* (fig. 8*B*). *Am. c-nigrum*, *T. pronuba* and the batch of species with two to five individuals form an intermediate type with a maximum between 10 and 20 feet (fig. 8*C*). Thus different species and groups of moths fly at different heights in the moderate wind speeds found at night up to 25 feet.

Commonness is also associated with height of flight. When *Amph. tragopoginis* was unusually common on two occasions and enough were caught to give profiles for single nights, they flew higher than usual (fig. 7*B*). Again, species represented by one individual only are caught predominantly in the lowest trap (fig. 8*A*); yet five out of the seven species with numbers sufficient to give individual profiles have a maximum above 10 feet (fig. 8*B*, *C*). The profile of density × height for the same species can also be compared at different times of night. Height profiles taken separately from the peak and tail of flight periodicity, show that *Ag. lychnidis* flies

high during the peak and low during the tail (fig. 9*A*). *Amph. tragopoginis* tends to do the same, but this is less evident as flight is always relatively low (fig. 9*B*). *X. monoglypha* has two peaks of flight periodicity of equal size, and these give identical height profiles (fig. 9*C*). As the difference in numbers between the peaks and the tails increases in each of these three examples, so also does the difference in height distribution. Again we find that, when a species is at its commonest, its flight is highest.

A possible explanation is that, in addition to the tendency of a particular species to fly at a given height, flight tends to be higher when climate is most suitable for flight, and hence when most fly.

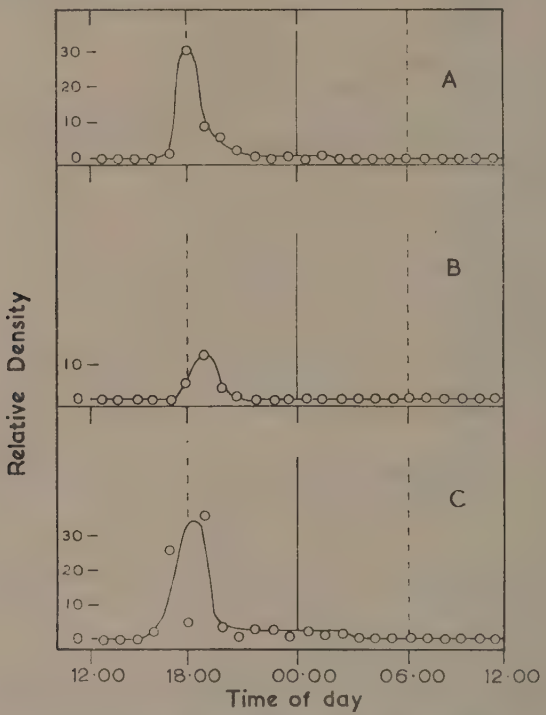

Fig. 5.—Flight periodicity of *Agrochola lychnidis* showing consistency of timing in three years 1953/4/5 : (*A*) 1953 ; (*B*) 1954 ; (*C*) 1955.

IV. Comparison of Light and Suction Trap Records

Suction traps have been very carefully standardised to ensure that the sample they obtain represents the population it is taken from (Taylor, 1955, and *in preparation*). In addition, enough evidence has been given here of the precise and repeatable results they give to justify their use as a standard of comparison for the use of light traps in population analysis.

(1) *The effect of light on the apparent commonness of moths*

Table III gives a list of species and their numbers in the light trap at Cardington during August and September, 1959. With it are compared the light trap catches of the same species for a corresponding period in 1934 at Rothamsted, 25 years before and 25 miles away. The catches have been summed in three groups to empha-

TABLE III.—*Comparison of species caught by suction trap and combined M.V. and tungsten filament light trap at Cardington, Beds., and by tungsten filament light trap at Harpenden, Herts.*

	Catch		
	Suction trap, Cardington	Light trap, Cardington	Light trap Rothamsted
Luperina testacea (Schiff.)	1	147	152
Amathes xanthographa (Schiff.)	0	134	100
Tholera popularis (Fabr.)	0	128	109
Amathes c-nigrum (L.)	9	127	82
Leucania pallens (L.)	2	53	29
Hydracia micacea (Esp.)	0	45	13
Diarsia rubi (Vieweg)	*1*	30	25
Amathes umbrosa (Hb.)	0	26	6
Gortyna flavago (Schiff.)	0	14	0
Hepialus sylvinus (L.)	0	14	8
Leucania impura (Hb.)	2	14	20
Trichiura crataegi (L.)	0	13	1
Triphaena pronuba (L.)	14	13	4
Phlogophora meticulosa (L.)	2	12	*6*
Xanthorhoë ferrugata (Cl.)	0 31	11 781	19 574
	—	—	—
Calothysanis amata (L.)	0	7	5
Plusia gamma (L.)	0	7	8
Deuteronomous fuscantaria (Haw.)	0	4	6
Hepialus lupulinus (L.)	0	4	1
Agrotis ypsilon (Rott.)	2	3	*1*
Chiasmia clathrata (L.)	0	3	2
Deuteronomous alniaria (L.)	0	3	3
Ochropleura plecta (L.)	0	3	4
Procus fasciunculus (Haw.)	*1*	3	*1*
Procus furunculus (Schiff.)	0	3	5
Agrochola lychnidis (Schiff.)	3	2	*2*
Agrotis segetum (Schiff.)	0	2	0
Aporophyla nigra (Haw.)	0	2	0
Cilix glaucata (Scop.)	0	2	3
Deuteronomous erosaria (Schiff.)	0	2	0
Lygris dotata (L.)	0	2	*1*
Opisthograptis luteolata (L.)	0	2	2
Petilampa minima (Haw.)	0	2	0
Tholera cespitis (Schiff.)	0 6	2 58	6 50
	—	—	—
Agrotis exclamationis (L.)	0	1	*1*
Abrostola tripartita (Hufn.)	0	1	*1*
Amphipyra tragopoginis (L.)	355	1	*2*
Caradrina taraxaci (Hb.)	0	1	0
Celaena secalis (L.)	1	1	3
Diataraxia oleracea (L.)	*1*	1	*1*
Dysstroma truncata (Hfn.)	0	1	1
Ectropis crepuscularia (Hb.)	0	1	0
Euproctis chrysorrhoea (L.)	0	1	2
Hadena chenopodii (Schiff.)	0	1	0
Heliophobus sordidus (Bork.)	0	1	*1*
Phragmatobia fuliginosa (L.)	1	1	1
Tethea duplaris (L.)	0	1	0
Triphaena comes (Hb.)	5	1	2
Xanthorhoë spadicearia (Schiff.)	*1*	1	0
Xylophasia monoglypha (Hufn.)	4 368	1 16	*2* 17
	—	—	—
N	405	855	641
S	17	50	40
α (per cent)	3·5±13	11·5±7·5	9·5±8·5

Figures in italics indicated moths caught at slightly different dates from the Cardington light trap record, *i.e.* 24th August to 14th September.

sise the similarity of the two sets of results. The first group contains insects of which more than ten were caught in the Cardington light trap ; the second group contains catches above one and below ten, and the third group consists of singletons. In both light traps group one is at least ten times as big as group two, which is three times as big as group three. The same insects occupy the first five places in the first group in each list.

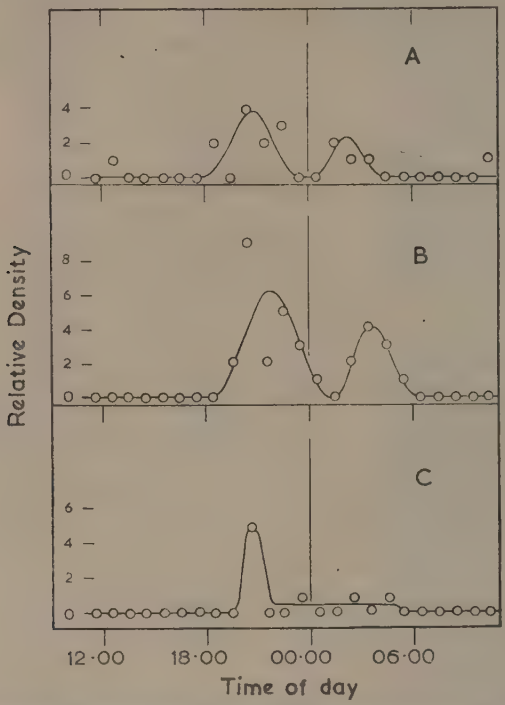

Fig. 6.—Flight periodicity of uncommon species : (*A*) summed catches of all species represented by 1 individual only ; (*B*) summed catches of species with 2–5 individuals (pseudobimodal periodicity) ; (*C*) *Apatele rumicis*, showing the typical " peak and tail " periodicity from a catch with only 8 individuals.

In contrast, the catches by suction trap for a corresponding period at Cardington, 100 yards from the light trap, are completely different. This may be caused partly by the difference in height of the traps ; the light trap at 2 feet 6 inches and the lowest suction trap at 9 feet. Neither interpolation from light traps at different heights (data from Williams, 1939), nor the data from suction traps in the present work, suggest that the commoner species at light would be greatly affected by this, but some very low flying species may be missed in the suction trap. Nevertheless the great difference shown in this table is, without doubt, attributable largely to the differential attractiveness of light for different species. If it is assumed that the effect of the difference in trap heights is similar for both species, then, because the suction trap catch is not biased, the light trap seems to be about (127/9)/(1/355) =5000 times as attractive to *Amathes c-nigrum* as to *Amphipyra tragopoginis*. If a differential effect of height is added, the factor is increased, as it is if *Luperina testacea* is considered instead of *A. c-nigrum* ; but the information about this species is less reliable. The factor of 5000/1 may be compared with (30·7/1)/(1/0·5) = 61/1 for the differential attraction of yellow water trays for two species of aphid (*Toxoptera*

citricidus (Kirkaldy) and *Acyrthosiphon pisum* (Harris) (Eastop, 1955) and (5474/1045)/(155/4815) = 162/1 for two groups of thrips (*Taeniothrips* spp. and *Limothrips cerealium* (Haliday) in white water trays (Lewis, 1959). The circumstances differ slightly; the aphids and thrips are drifting past the traps in the wind and so the selection of the colour trays operates on the same populations as are sampled by the suction traps. There is no evidence that this is true for light traps. The moths are

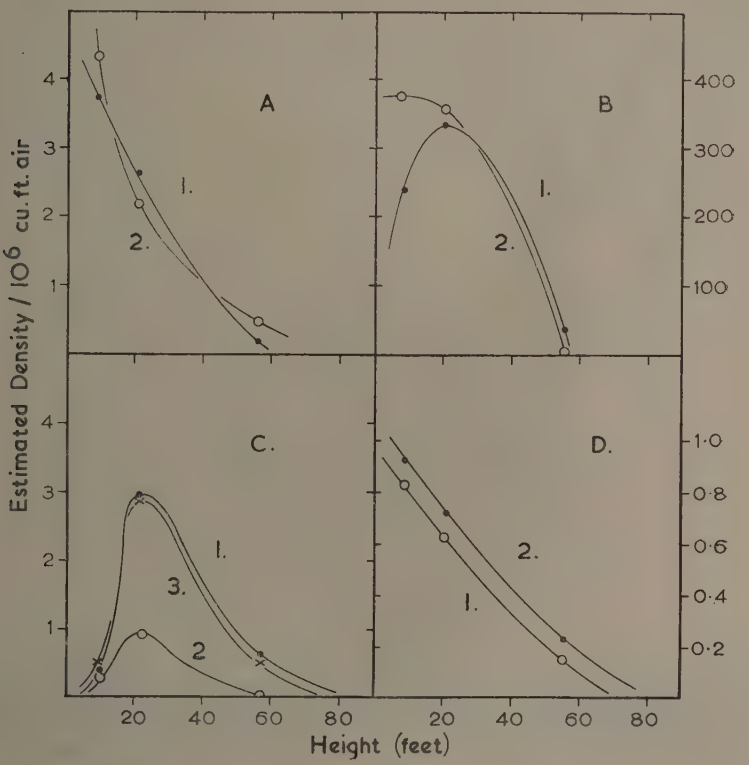

FIG. 7.—Height of flight of Macrolepidoptera for separate days and separate years. (*A*) *Amphipyra tragopoginis*: (1) 1954; (2) 1955. (*B*) *Amphipyra tragopoginis*: (1) 26–27th August, 1954; (2) 27–28th August, 1954. (*C*) *Agrochola lychnidis*: (1) 1953; (2) 1954; (3) 1955. (*D*) Other Heterocera combined: (1) 1954; (2) 1955.

flying mainly under their own control and one species may be more sedentary than another, so that the effective area of influence of the light trap may differ for the two species without affecting the real density as measured by the suction trap.

The wide area of influence of the light trap is shown by the index of diversity: $\alpha = 11{\cdot}5 \pm 7{\cdot}5$ per cent. compared with $\alpha = 3{\cdot}5 \pm 13$ per cent. for the same time and place measured by suction trap; this is the great asset of a light trap for sampling Macrolepidoptera but it does make it unsuitable for comparing the relative commonness of different species in the same place, although it does not detract from its importance in comparing the relative commonness of the same species in different places and on different occasions, provided lunar periodicity is taken into account (*see below*). Obviously the light trap is highly suited to investigating the phenology and geographical distribution of species or for any other subject requiring mainly a record of the presence of a species.

(2) *Effect of light on apparent distribution*

(*a*) *Time of flight*

The sampling power of the light trap varies from a minimum in full daylight to a maximum at midnight on moonless nights. Light trap catches vary sensitively with the height of the moon and with the lunar cycle (Williams, 1936). Suction

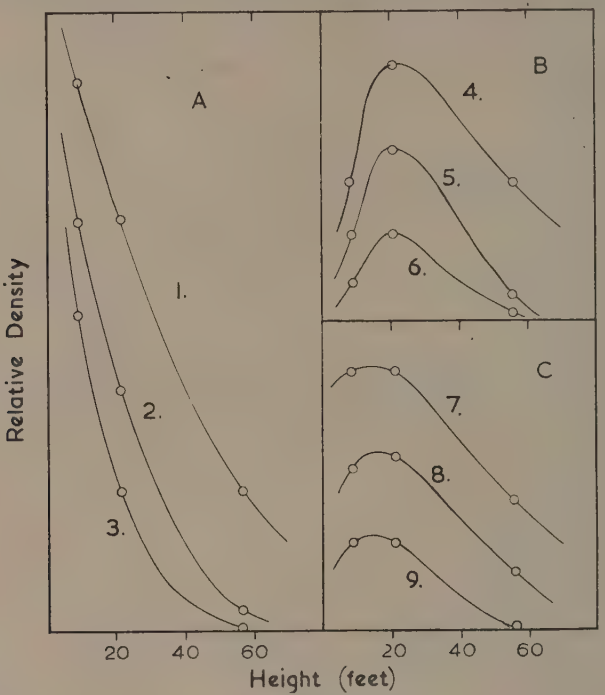

Fig. 8.—Height of flight for all years combined ; the ordinates for the curves have been staggered and scales varied to avoid overlapping. (*A*) : (1) *Apatele rumicis ;* (2) *Amphipyra tragopoginis ;* (3) species with 1 individual, combined. (*B*) : (4) *Euxoa nigricans ;* (5) *Xylophasia monoglypha ;* (6) *Agrochola lychnidis.* (*C*) : (7) *Triphaena pronuba ;* (8) species with 2–5 individuals, combined ; (9) *Amathes c-nigrum.*

trap catches do not (Williams, Singh and El Ziady, 1956). A similar effect of moonlight has also been recorded in light trap catches of mosquitoes by Provost (1959). The variability in the catches of the light trap is caused by competition with a moon of given phase appearing in the sky either at different times or for different lengths of time (Williams, 1936). If the light trap is sufficiently sensitive to record this, it is not surprising that the apparent diurnal periodicity of flight of insects, as measured by a light trap, is not realistic for species attracted to light. Figure 10 shows the periodicity of flight of six species of moths measured by suction trap and by light trap (data of Williams, 1935). That some of the catches are very small does not prevent a clear comparison.

The first four species, *Xylophasia monoglypha*, *Triphaena pronuba*, *Agrochola lychnidis* and *Amathes c-nigrum*, are all strongly attracted to light, at least during some phase of adult life. The true periodicity, shown by suction traps, is grossly distorted by the light traps and needs no further comment (fig. 10*A*, *B*, *C*, *D*).

Amphipyra tragopoginis and *Euxoa nigricans* are not strongly attracted to light and little can be said about *E. nigricans* (fig. 10*E*) for only three were caught in

four years; however the trend is the same as for *Amph. tragopoginis* (fig. 10*F*). This is a very common insect, and therefore the small number caught in the light trap (nine in four years) suggests that its visits were not directly motivated by light, but were possibly chance encounters. This is emphasised by their periodicity, which is a reasonable reflection of the numbers flying as measured by suction trap. Records

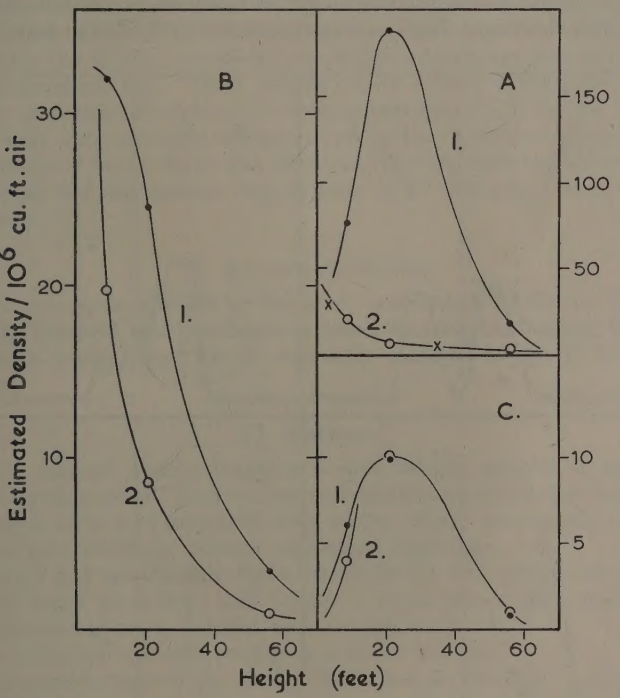

FIG. 9.—Height of flight at different times of night. (*A*) *Agrochola lychnidis*: (1) peak period of flight 15.00–20.00 hours; (2) tail of flight 21.00–03.00 hours. (×, relative light trap catches.) (*B*) *Amphipyra tragopoginis*: (1) peak period of flight 19.00–23.00 hours; (2) tail of flight 00.00–05.00 hours. (*C*) *Xylophasia monoglypha*: (1) first peak of flight 19.00–00.00 hours; (2) second peak of flight 01.00–05.00 hours.

of nine insects caught by chance are more valuable than many hundreds artificially attracted when the attraction is itself caused by the same variable whose supposed independent effect on abundance is being considered; as an instrument for measuring flight periodicity, the light trap is only effective for those insects not attracted to light!

(*b*) *Height of flight*

Williams (1939) studied the height of flight of Macrolepidoptera, using a second light at 36 feet in addition to the standard trap at 3 feet 6 inches. Unfortunately, with only two heights, profiles cannot be drawn because a maximum might occur between these two widely spaced traps and would not be recorded. There is, however, a second and more serious difficulty. Because moths fly at different heights at different times of night and the catches in the light trap distort diurnal periodicity of flight, the light trap often catches most moths at times other than when most are flying. For example, most *X. monoglypha* are caught between midnight and 02.00 hours, when flight activity is actually depressed (fig. 10*A*). This makes it very difficult to verify the validity of height distributions by light trap.

The suction trap shows that most *Ag. lychnidis* fly between 15.00 and 20.00 hours, and at about 20 feet; there is a tail of flight between 21.00 and 03.00 hours, comprising a few which fly mainly below 9 feet. The light trap catch is greatest during this latter period (21.00–03.00 hours, fig. 10*C*) and the insects flew predominately at low levels, *i.e.* more at 3 feet 6 inches than at 36 feet, conforming with the insects in the tail of flight profile (21.00–03.00) as measured by suction trap (fig. 9*A*). This shows that the height distribution as measured by light trap is valid, but taking

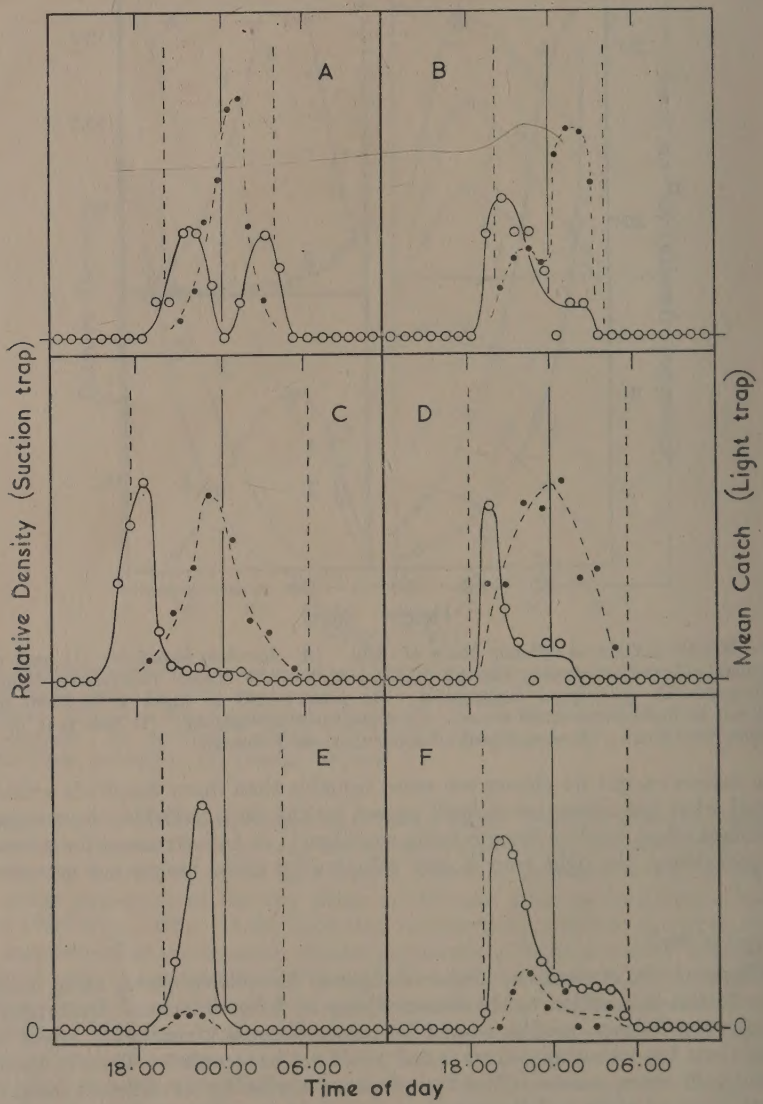

Fig. 10. Flight periodicity of six insect species to various scales chosen for convenience in illustration. (——○—— measured by suction trap; – – ● – – erroneous periodicities by tungsten filament light trap, caused by changing efficiency of trap as background light changes.) (*A*) *Xylophasia monoglypha*; (*B*) *Triphaena pronuba*; (*C*) *Agrochola lychnidis*; (*D*) *Amathes c-nigrum*; (*E*) *Euxoa nigricans*; (*F*) *Amphipyra tragopoginis*.

the night as a whole instead of considering the 15.00–20.00 and 21.00–03.00 hours separately, the light trap again gives a misleading result. This is because it obtains its catch during those hours when only 10 per cent. of the population, which are atypical of the population as a whole, are in flight; this 10 per cent. fly low, the remaining 90 per cent. fly high.

The analysis of this species shows the value of the suction trap most clearly. With a total catch of only 169 insects in three years, it is possible to define accurately and consistently the diurnal periodicity, the flight temperature threshold, the height of flight and the phenology. These aspects can be defined statistically with limits, if necessary; at present the labour involved seems unjustified, for the flight of this species is already very narrowly circumscribed by the definitions given graphically. But as the study of insect flight and dispersal proceeds, such statistical limits may become essential and the suction trap appears to be the only current method for obtaining them.

V. Acknowledgments

This work was made possible by the kind co-operation of Mr. L. A. Speed and the staff of the Research and Development Establishment, Cardington, Bedfordshire, where the traps worked, and we are especially indebted to Mr. E. G. Jones who changed them.

VI. Summary

1. In three seasons' suction trapping at five heights, population structure was found to be very consistent. Most species were resident but there was some migration.

2. Butterflies were rare compared with moths, which occasionally reached very high densities, comparable in biomass with aphid migrations.

3. Phenology and temperature flight thresholds for two species are given.

4. Diurnal flight periodicity and height of flight were highly specific with an interaction between them associated with population level.

5. No Macrolepidoptera were caught at or above 250 feet.

6. Light traps selected certain species 5000 times as strongly as others.

7. The efficiency of light traps varies greatly during the night so that flight periodicity cannot usefully be measured by them.

8. It is also very difficult to use light traps to measure height of flight because of the interaction with flight periodicity. The light trap catches *Agrochola lychnidis* only at times when about 10 per cent. are in flight and the mean height of flight is below 9 feet; the mean height of flight of the remaining 90 per cent. is above 20 feet.

9. With a suction trap catch of only 169 specimens in three years, the flight temperature threshold, height of flight, diurnal periodicity and phenology of *Ag. lychnidis* could be accurately defined.

VII. References

Eastop, V. F., 1955, Selection of aphid species by different kinds of trap. *Nature, Lond.* **176**: 936.

Giblett, M. A. and others, 1932, The structure of wind over level country. Report on experiments carried out at the Royal Airship Works, Cardington. *Met. Off. geophys. Mem.* **54**, 6 (4): 1–119.

Johnson, C. G., 1952, The changing numbers of *Aphis fabae* Scop., flying at crop level, in relation to current weather and to the population on the crop. *Ann. appl. Biol.* **39**: 525–47.

—— 1957, The distribution of insects in the air and the empirical relation of density to height. *J. anim. Ecol.* **26**: 479–94.

—— and Taylor, L. R., 1955*a*, The development of large suction traps for airborne insects. *Ann. appl. Biol.* **43**: 51–62.

Johnson, C. G. and Taylor, L. R. 1955*b*, The measurement of insect density in the air. *Lab. Pract.* **4** : 187–192, 235–39.

Kloet, G. S. and Hincks, W. D., 1945, *A check list of British Insects.* Stockport.

Larsen, E. B., 1943, The importance of master factors for the activity of noctuids. Studies on the activity of insects, 1. *Ent. Medd.* **23** : 352–74.

Lewis, T., 1959, A comparison of water traps, cylindrical sticky traps and suction traps for sampling thysanopteran populations at different levels. *Ent. exp. appl.* **2** : 204–15.

Mel'nichenko, A. N., 1936, Regularities of mass flying of the adults of *Loxostege sticticalis* L. and the problem of the prognosis of their flight migrations. *Bull. Plant Prot.* (1) *Ent.* No. 17, 56 pp. [*In Russian.*]

Provost, M. W., 1959, The influence of moonlight on light trap catches of mosquitoes. *Ann. ent. Soc. Amer.* **52** : 261–71.

Taylor, L. R., 1955, The standardization of airflow in insect suction traps. *Ann. appl. Biol.* **43** : 390–408.

—— 1957, Temperature relations of teneral development and behaviour in *Aphis fabae* Scop. *J. exp. Biol.* **34** : 189–208.

—— 1960, The distribution of insects at low levels in the air. *J. anim. Ecol.* **29** : 45–63.

Williams, C. B., 1935, The times of activity of certain nocturnal insects, chiefly Lepidoptera, as indicated by a light trap. *Trans. R. ent. Soc. Lond.* **83** : 523–55.

—— 1936, The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap. *Phil. Trans.* (B) **226** : 357–89.

—— 1939, An analysis of four years' captures of insects in a light trap. Part I. General survey ; sex proportion ; phenology ; and time of flight. *Trans. R. ent. Soc. Lond.* **89** : 79–132.

—— 1947, The logarithmic series and its application to biological problems. *J. Ecol.* **34** : 253–72.

—— 1948, The Rothamsted light trap. *Proc. R. ent. Soc. Lond.* (A) **23** : 80–85.

—— Singh, B. P. and El Ziady, S., 1956, An investigation into the possible effects of moonlight on the activity of insects in the field. *Ibid.* **31** : 135–44.